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Artículo Original

GROWTH AND COMPENSATORY GROWTH OF *Lutreolina crassicaudata* (MARSUPIALIA-DIDELPHIDAE) UNDER ANIMAL FACILITY CONDITIONS

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ABSTRACT. Biomedical research has utilized marsupials, such as *Didelphis* and *Lutreolina*, as Non-Traditional Laboratory Animals (NTLAs) for years. While *Didelphis* is widely recognized, *Lutreolina*, another genus of opossums, also holds value in biomedicine. However, understanding its growth and physiological development remains a challenge. This study focused on the growth of three litters of *L. crassicaudata*, which were obtained from the controlled breeding of animals raised in captivity for three successive generations. Nine males and ten females were weighed from artificial weaning to 80 weeks, and their growth was modeled using the Gompertz function separately for each sex. Additionally, one litter underwent a ten-week dietary restriction as part of a parallel behavioral study, and its compensatory growth was assessed. The results revealed clear sexual dimorphism, with males exhibiting higher growth rates than females. The Gompertz model provided a good fit for the growth data (parameters: male A = 968.8 ± 22.21 g, k_G = 0.05 ± 0.0034, T_i = 24.22 ± 0.764 wk; female A = 433.8 ± 3.95 g, k_G = 0.06 ± 0.0025, T_i = 16.82 ± 0.450 wk). The litter subjected to dietary restriction experienced delayed weight gain. This study highlights the growth pattern of *L. crassicaudata*, resembling that of other mammals, and demonstrates that early dietary restriction led to compensatory growth when normal feeding resumed. These findings contribute to a better understanding of the growth of marsupials used in biomedical research and their adaptability to experimental conditions.

RESUMEN. CRECIMIENTO Y CRECIMIENTO COMPENSATORIO DE *Lutreolina crassicaudata* (MARSUPIALIA-DIDELPHIDAE) EN CONDICIONES DE BIOTERIO. La investigación biomédica ha utilizado marsupiales, como *Didelphis* y *Lutreolina*, como Animales de Laboratorio No Tradicionales (ALNT) durante años. Aunque *Didelphis* es ampliamente conocido, *Lutreolina*, otro género de zarigüeyas, también es valioso en la biomedicina. Sin embargo, se enfrenta al desafío de comprender mejor su crecimiento y desarrollo fisiológico. Este estudio se centra en el crecimiento de tres camadas de *L. crassicaudata*, obtenidas de la cría controlada de animales criados en cautiverio durante tres generaciones sucesivas. Se pesaron nueve machos y diez hembras desde el destete artificial hasta las 80 semanas, y su crecimiento se modeló utilizando la función de Gompertz por separado para cada sexo. Además, una camada experimentó una restricción alimentaria durante diez semanas para un estudio comportamental paralelo, y se evaluó su crecimiento compensatorio. Los resultados revelaron un claro dimorfismo sexual, con un crecimiento superior en los machos en comparación con las hembras. El modelo de Gompertz ajustó bien los datos de crecimiento (parámetros: machos A = 968,8 ± 22,21 g, k_G = 0,05 ± 0,0034, T_i = 24,22 ± 0,764 sem; hembras A= 433,8 ± 3,95 g, k_G = 0,06 ± 0,0025, T_i = 16,82 ± 0,450 sem). La camada con restricción alimentaria experimentó un retraso en la ganancia de peso. Este estudio destaca el patrón de crecimiento en *L. crassicaudata* similar a otros mamíferos, y muestra que la restricción alimentaria inicial llevó a un crecimiento compensatorio cuando se restauró la dieta normal. Estos hallazgos contribuyen a comprender mejor el crecimiento de marsupiales utilizados en investigación biomédica y su capacidad de adaptación a las condiciones experimentales.

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Palabras clave: Crecimiento animal, *Lutreolina*, zarigüeya colorada, modelo de Gompertz, reproducción marsupiales en bioterio, animales de laboratorio no tradicionales.

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INTRODUCTION

Laboratory Animals require a deep understanding of their biology and clinical-physiological reference parameters to ensure the reliability of experimental results derived from their use. While this is already a significant challenge, animal care specialists and researchers who utilize new animal species as experimental models and adapt their housing conditions to laboratory facilities face even greater difficulties. This choice often involves wild animals, leading to the development of Non-Traditional Laboratory Animals (NTLA) (Iodice 1987, 1988, 2013; Iodice & Cervino 2019, 2020).

NTLA is a term we coined years ago to identify new animal models used in biomedical research and raised in laboratory environments, as opposed to those used in field experiments (Iodice & Cervino 2023).

One of the main challenges for scientists raising their models in laboratories is obtaining animals of known age and parental characteristics and estimating appropriate weight gain according to their age and growth rate. The individual growth of specimens requires special attention to ensure proper colony management.

Animal Growth and Development

Body growth and development encompass a series of intricate anatomical, physiological, and behavioral changes in an organism. These terms are often conflated and used interchangeably, despite being interdependent yet distinct processes, making their precise definition challenging.

Fowler (1968) distinguishes two key aspects of growth: (a) the increase in body mass (weight) over time and (b) changes in body composition and shape resulting from the differential growth of various anatomical structures.

However, we consider the definitions proposed by Ayala Vargas (2018) to be more precise. Building on Hammond (1960), Ayala Vargas defines growth as the increase in weight from birth until reaching stability in adulthood, whereas development encompasses modifications in the morphology, biochemistry, and physiology of the animals over time. According to these authors, growth and development generally occur simultaneously and in a coordinated manner. However, exceptions exist, such as individuals that continue to develop (e.g., increasing in height or length) without significant weight gain or fully developed adult animals that experience weight gain due to fat accumulation.

Brody (1945) considers growth as the result of biological synthesis, which encompasses three key processes: (a) hyperplasia, which refers to growth through an increase in cell numbers (cellular multiplication); (b) hypertrophy, which involves growth through an increase in cell size, and (c) accumulation, which is the incorporation of materials such as fat and blood plasma. These biological processes may occur simultaneously or separately, depending on the growth stage. For example, during the prenatal growth phase (between fertilization and birth), hyperplasia predominates, while hypertrophy and material accumulation become more significant as growth progresses (Ferchichi et al. 2022).

Anabolic hormones facilitate growth, including (Forsyth 1986; Ayala Vargas 2018): somatotropin (growth hormone, GH), thyroid hormones, insulin, androgens, estrogens, glucocorticoids, prolactin, placental lactogen, and parathyroid hormone.

The most common growth measurement is body weight, although other body size measurements (height, length, or, as in humans, head circumference) can also be used. In this sense, growth can be defined through (Ayala Vargas 2018; Hutu et al. 2020): 1) total growth curve or cumulative weight gain; 2) weight increase per unit of time, and 3) percentage of weight gain per unit of time or relative weight gain.

In mammals, the growth rate decreases significantly from embryogenesis to young adulthood. For example, in humans, this deceleration is most pronounced during infancy, followed by a more subtle decline through middle childhood, interrupted by a pubertal growth spurt, after which the growth

rate gradually decreases to zero (Guimarey 2001; Rosenbloom 2007).

Like other biological processes, growth and development are shaped by both intrinsic factors (e.g., genetics, age, sex, and hormones) and extrinsic factors (e.g., climate, diet and nutrition, management, and intra/inter-species competition) (Guimarey 2001; Alemneh & Getabalew 2019; Hutu et al. 2020). The extent of growth and development achieved in adulthood is determined by hereditary, idiosyncratic, and nutritional factors, requiring a well-coordinated progression of the entire organism. These principles apply to both intrauterine and extrauterine growth. Additionally, the growth rate of the animals is primarily influenced by their age, adult weight, and sex (Ayala Vargas 2018).

Growth models: Mathematical properties

The growth curve of mammals is expected to follow a general pattern with a sigmoid shape, reaching asymptotic values at a species-specific age (Ayala Vargas 2018). This pattern is commonly described by the "logistic curve" or "logistic function". Various models have been proposed to characterize this growth trajectory (Agudelo-Gómez et al. 2007; Ferchichi et al. 2022). Table 1 presents the main nonlinear statistical models used for describing animal growth.

Furthermore, several authors propose the Michaelis-Menten equation, widely used to mathematically describe various chemical reactions, as a tool for plotting curves to describe animal growth (López et al. 2000; Iglesias et al. 2007).

The growth curve for mammals generally follows a sigmoid or S-shaped pattern (Ayala Vargas 2018), reaching asymptotic values at a specific age for the species. It can be represented by a graph with three distinct phases (**Fig**. 1):

a) Initially, the curve exhibits slow growth, referred to as the lag phase (I), corresponding to the early growth period.

b) This is followed by a rapid or exponential growth phase, known as the logarithmic phase (II), indicating a period of accelerated exponential growth.

c) Finally, the curve reaches a plateau or stabilization phase (III), where the upper level is indicated by a constant, representing the upper asymptote of the sigmoid curve, a more or less balanced and stable level.

In addition to dividing the curve into three phases based on its slope, it can also be analyzed by dividing it into two stages at the inflection point (Ferchichi et al. 2022). The first part of the characteristic sigmoid curve (self-acceleration stage) shows that during the early stages of growth, the increase in body mass significantly exceeds losses. This remains consistent during this stage, and the weight gain is linear in relation to age. In the second part (self-inhibition stage), the curve reflects the animal's approach to adulthood, where the rates of body mass gain and loss tend toward equilibrium. Thus, the growth curve asymptotically approaches a stable value. Some authors consider the inflection point to correspond to the onset of puberty (Brody 1945; Fowler 1968).

Selection of the growth model

Animal growth has been described using various mathematical functions (see **Table** 1). The Gompertz model (Gompertz 1825) is one of the most widely used sigmoid models, fitting data on animal growth, microbial colony expansion, tumor progression, and more (Enderling & Chaplain 2014; Avraam et al. 2016; Heesterman et al. 2019; Wang & Guo 2024). The Gompertz equation effectively models self-regulated growth patterns. In these cases, after reaching the inflection point, the growth rate decreases exponentially over time. The corresponding growth curve is sigmoid (see **Fig**. 1), characterized by an inflection point (representing the maximum growth rate relative to age) and an asymptote (Lawrence & Fowler 2002).

Several forms of the Gompertz model can be found in the literature. Another valuable parameterization, distinct from that presented in **Table** 1 and commonly encountered in studies, is (Tjørve & Tjørve 2017):

$$W_{(t)} = A \cdot e^{(-e^{(-k_G \cdot (t - T_i))})}$$

where $W_{(t)}$ is the expected weight of the animal as a function of time (e.g., days or weeks since birth), and t represents time. The parameter A (A > 0) represents the adult weight of the animal (the upper asymptote), k_G (k_G > 0) is the relative growth rate (affecting the slope), and T_i represents the time at the inflection point of the growth curve.

The parameter k_G provides an estimate of maturity precocity (Nobre et al. 1987); the higher its value, the earlier the animal matures, and vice versa (Brown et al. 1976). The value T_i is often considered a location parameter, as it horizontally shifts the growth curve without altering its shape. In contrast, A and k_G

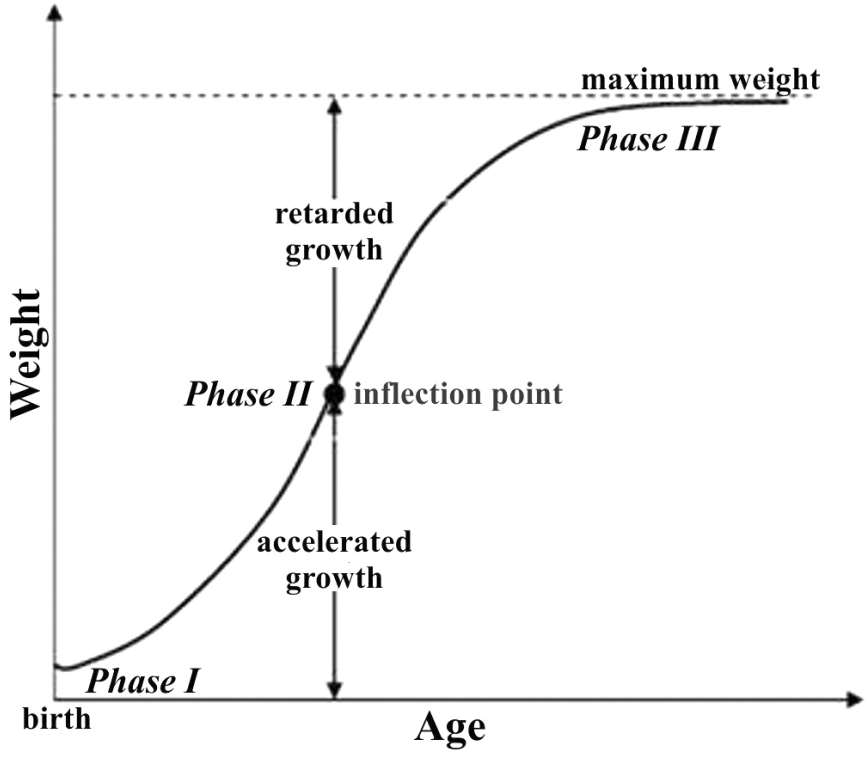

Fig. 1. Changes in body weight with age. It represents the cumulative growth curve, sigmoidal in shape and similar to the logistic growth curve of the population.

are shape parameters that, together with T_i, define a type I model (Tjørve & Tjørve 2017). Although the Gompertz model is highly useful, it rests on a key assumption: that weight eventually reaches an asymptote.

The key mathematical properties of the Gompertz model are detailed in Casas et al. (2010) and Tjørve & Tjørve (2017).

The Gompertz model has been applied to study the growth of several mammal species, such as mice (Kurnianto et al. 1998), rabbit (Setiaji et al. 2013), rat (Vázquez-Borsetti 2024), goat (Makgopa et al. 2023) and sheep (Foroutanifar & Khaldari 2024; de Assunção et al. 2024).

Compensatory growth

Compensatory growth (CG) is a biological phenomenon observed in many animal species. CG is characterized by a rapid increase in the growth rate relative to age following a period of restriction, typically due to reduced feeding (Wilson & Osbourne 1960; Hornick et al. 2000; Hector & Nakagawa 2012; Deng et al. 2024). **Figure** 2 illustrates the growth curves of an animal with normal feeding and one subjected to a period of underfeeding in the interval t_1–t_2. CG manifests as an "abnormally" high growth rate during the recovery period.

Consequently, CG involves a sharp acceleration in growth velocity once the feeding restriction is removed, followed by a gradual deceleration until normal growth velocity is achieved when the animal regains its expected size or weight. CG is a physiological recovery process relevant in both animal production and human clinical contexts.

In the context of animal production (Carstens et al. 1991; Yambayamba et al. 1996; Luna-Pinto & Cronjé 2000), CG has been employed as a strategy to manage costs and/or the characteristics of seasonal feeding through the nutrition-feeding relationship in production animals. In clinical settings, CG refers to the accelerated growth observed in children who have experienced growth retardation due to specific factors (malnutrition, diseases, etc.). The term "catch-up growth" was introduced by Prader et al. (1963) and

Table 1

General form of non-linear models to estimate animal growth.

Model	Mathematical expression
Gompertz (1825)	$y = Ae^{-Be^{-kt}}$
Brody (1945)	$y = A(1 - Be^{-kt})$
Von Bertalanffy (1938, 1957)	$y = A(1 - Be^{-kt})^3$
Richards (1959)	$y = A(1 - Be^{-kt})^m$
Logístico (Nelder 1961)	$y = A(1 + e^{-kt})^{-1}$

y: growth of the organism; A: adult weight of the animal as time tends to infinity; B: integration factor that adjusts initial weight values and is generally associated with birth weight; k: maturity rate, function between the maximum growth rate and the adult weight of the animal; t: time or age; m: inflection point.

Tanner (1963) in the early 1960s. Once the underlying causes are resolved, growth recovery occurs.

Animal model: *Lutreolina crassicaudata*

Marsupials (infraclass: *Marsupialia*) are a group of mammals that currently inhabit only the Americas and Oceania (Nilsson et al. 2004). Despite significant external differences, both communities share the remarkable characteristic of carrying their offspring within a fold of skin that encloses the mammary glands (*marsupium*) for much of their ontogenic development (Smith & Keyte 2020).

L. crassicaudata is a South American marsupial commonly known as the red opossum ("zarigüeya colorada") or thick-tailed opossum ("coligrueso") (Muschetto et al. 2011; Martin & Flores 2019). It is also referred to as the little water opossum or lutrine opossum. It is often incorrectly called the "American weasel", a misnomer since weasels are eutherian mammals of European origin rather than marsupials. Until recently, it was considered the only extant representative of the genus *Lutreolina*. Its distribution includes two distinct regions: a southern zone encompassing eastern Paraguay, central and northeastern Argentina, southern Brazil, and Uruguay, and a northern range covering parts of Colombia, Venezuela, and Guyana (Marshall 1978; Martin & Flores 2019). However, Martínez Lanfranco et al. (2014) described a second living species in the montane forest regions (Yungas) of northwestern Argentina and southwestern Bolivia, identified as *L. massoia*.

When compared to the growth curve of all mammals, marsupials exhibit a slower growth rate (Lee & Cockburn 1985; Cockburn & Johnson 1988). This may be attributed to the gradual postnatal maturation of the GH/IGF-I axis in marsupials (Menzies et al. 2012). However, according to these authors, complete maturation occurs at the same relative developmental stage as in eutherian mammals. Notably, growth axis maturation in marsupials is not linked to birth.

Both *L. crassicaudata* and other marsupial species of the genus *Didelphis* have been extensively studied and developed as experimental models, including as NTLA models, both in Argentina and worldwide (Jurgelski 1974, 1979; Jurgelski & Porter 1974; Jurgelski et al. 1974; Iodice et al. 1985, 1988a,b,c, 2007, 2010; Iodice 1987, 1988, 2010, 2013; Iodice & Affanni 1988; Bianchini et al. 2020; Iodice & Cervino 2019, 2020, 2023).

Study objectives

This study aims to achieve the following objectives:

a) to investigate the growth patterns and weight gain in marsupials of the species *Lutreolina crassicaudata* born in captivity, under facility conditions, and through programmed mating;
b) to describe their growth using the parameterization of the Gompertz model; and
c) to analyze the phenomenon of compensatory growth, or catch-up growth, in this species, with a particular focus on early growth stages.

MATERIALS AND METHODS

The species used in this study was the thick-tailed opossum, *Lutreolina crassicaudata* (Mammalia, Didelphidae). The specimens belonged to the Marsupial and Armadillo Colony of the Institute of Neuroscience (INEUCI-CONICET), housed in the Central Animal Facility at the Faculty of Exact and Natural Sciences, University of Buenos Aires (UBA).

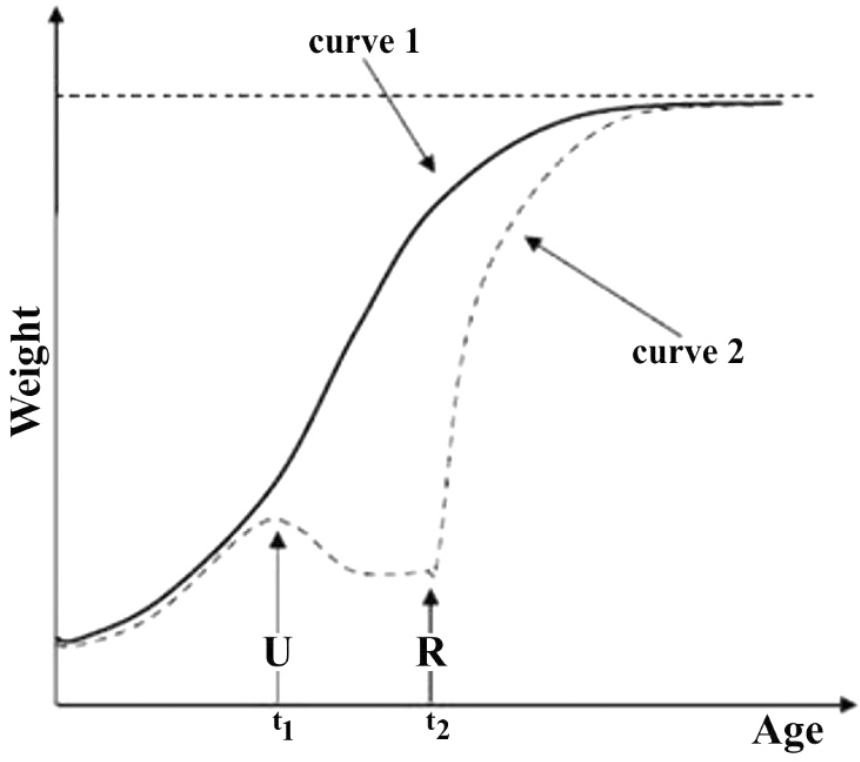

Fig. 2. Compensatory growth curve of an animal that was subjected to a period t_1-t_2 of underfeeding (curve 2) compared to the growth curve of another with normal feeding (curve 1). U-R segment, restriction (U, onset of underfeeding; R, start normal eating or rehabilitation); R-asymptote segment, compensatory growth.

Three litters of pups born in the facility were used, originating from three different females born in the colony and mated according to a programmed schedule. These females were adult animals fully adapted to the controlled conditions of the facility.

Mating was scheduled by performing exfoliative vaginal cytology sampling stained using the modified Papanicolaou method (Iodice et al. 1988a,b, 2007, 2010). After identifying the estrous stage using the "superficial cell" and "acidophilic" indices (Schutte 1967), the females were mated with preselected males for no more than 3-4 days. This prior selection of males aimed to establish open breeding lines to prevent inbreeding in the colony (Iodice et al. 1988a,b, 2007, 2010).

From the 10th day after the first mating, the pouches of the females were checked daily until the presence of pups in the marsupial pouch was observed. The condition of the newborns within the pouch was monitored every 4-5 days starting from the day of birth. Three litters born in October, November, and December (Southern Hemisphere spring) were selected for the study and designated as Litter I, II, and III, respectively.

At 12 weeks of age, the pups were weaned and housed individually. The decision to wean at this time was based on observations from earlier litters in our breeding facility, outside of controlled reproductive programs. Between 12 and 14 weeks of age, the juveniles exhibited aggressive behavior toward the mother, causing significant injuries and, in some cases, death. These incidents occurred out of the immediate observation of personnel. This aggression coincided with the reduction in size and productivity of the maternal mammary glands. Simultaneously, juveniles began to share the balanced diet of the mothers progressively, starting one to two weeks earlier. These factors led to the decision to wean at the specified time.

Weights were not recorded during the pouch stage due to the close adhesion of juveniles to the teat of the mother, nor during free lactation, as individual identification was challenging, and there was a risk of group aggression based on prior experiences.

At weaning, juveniles were housed individually. They were placed in wire cages measuring 44 × 32 × 25 cm (length, width, and height, respectively), commonly referred to as collective rat cages (**Fig**. 3). The technique of gradual separation was not implemented due to concerns about aggression among siblings.

They were fed high-nutrition puppy chow. The general composition of the food used to feed *L. crassicaudata* pups included chicken meal, bovine meat meal, chicken fat, first-rendering bovine tallow, enzymatic hydrolyzed chicken,

Fig. 3. Specimen of *Lutreolina crassicaudata* housed in an individual cage, with a container with food and a “bottle-type” drinker.

corn, rice, soybean meal, wheat germ, barley, chicory pulp, and yucca extract. Minerals included calcium chloride, zinc oxide, manganese oxide, ferrous sulfate, calcium iodate, copper oxide, and sodium selenite. Vitamins and essential elements included A, D_3, E, K_3, B_1, B_6, B_{12}, calcium D-pantothenate, nicotinic acid, folic acid, choline, biotin, lysine, methionine, and antioxidant (BHT). The proportional composition of the chow was as follows: maximum moisture, 12%; minimum crude protein, 27%-30%; digestible protein (minimum), 17%; minimum ether extract, 15%; maximum crude fiber, 2.8%-3.0%; ash, 9%; calcium, 1.3%-1.6%; phosphorus, 0.9%-1.3%, and metabolizable energy, 4 100-4 200 kcal/kg DM. The pups were provided with 100-150 g of food daily, depending on sex and age. Water was offered ad libitum using inverted “bottle-type” drinkers as used for laboratory rodents.

Environmental conditions for maintenance were as follows: temperature, 24 ± 3 °C; natural humidity without regulation, and a light-dark cycle of 12:12, with lights on at 7:00 a.m.

The weights of the pups were measured weekly starting from weaning and continued for 80 weeks using a triple-beam balance (precision: 5 g).

It was not feasible to weigh the pups from birth due to the peculiar lactation process in marsupials, which occurs in two stages: a phase of permanent attachment followed by intermittent suckling. The first six weeks of lactation, referred to as the "pouch-lactation period" (typical of marsupials), involve a permanent connection between the mouth and the teat of the neonate, which, if disrupted, cannot be re-established, leading to the death of the pup. During the subsequent six weeks, known as the "free-lactation period" (comparable to placental mammals), although individual access to the pups was possible, handling was avoided to prevent the mothers from rejecting or harming the pups due to unfamiliar scents.

As a result, the pups were weighed starting at 12 weeks of age and continued until they were 23 months old (one year and 11 months).

During this study, the pups from Litter I participated in an operant conditioning experiment focused on behavior between weeks 47 and 57 of life. For this, their food intake was reduced to 80% of their regular ration. After the ten-week experimental period, the animals were withdrawn from the behavioral study, and their feeding returned to normal. Weight evolution was monitored throughout this period, despite being under a different experimental design. CG was evaluated by checking the general tendency of the growth curve (weight vs. time) to recover its normal characteristics after the adverse feeding period.

The degree of CG was quantified using the "compensatory index" (Hornick et al. 2000), calculated as the ratio of the difference in weight change at the end of the restricted and CG phases, respectively, relative to the change at the end of restricted growth only (Wilson & Osbourne 1960). A value of 100% indicates full recovery, although this is rarely observed; typically, the index value ranges between 50% and 100% (Hornick et al. 2000).

The growth of the animals was modeled using the Gompertz equation, as described in the Introduction. This

model has three parameters (A, k_G, and T_i), and its mathematical expression is shown in Equation 1. To estimate the growth curve and its parameters, the Gompertz model was fitted using the Sigmoidal Curve Fit procedure in OriginPro (2016, OriginLab Corporation). Data fitting and parameter estimates were performed using the Levenberg-Marquardt iterative algorithm in the non-linear modeling procedure of OriginPro.

The Ethics Committee of the Institute of Neurosciences (INEUCI-CONICET) granted ethical approval for the project. The animals were housed and used in accordance with the ethical guidelines of the Canadian Council on Animal Care (https://www.ccac.ca/en/standards/guidelines/). Current Argentine regulations, provisions, and international legislation were also observed.

RESULTS

As mentioned in Material and Methods, starting on the tenth day after the first pairing, a scheduled daily control of the females' marsupial pouches was carried out until the presence of offspring was observed in them. In *Lutreolina*, under captive breeding conditions, births occur between 13 and 15 days post-mating.

The data collected over 80 weeks were recorded in tables categorized by litter and sex (Table S1). Below, the values are presented in graphs by sex and litter.

Figure 4 shows the distribution of body weight (g) versus age (weeks), differentiating between males and females, for Litters II and III. Throughout the weight monitoring period, no changes were observed in the thickness of the tails of the animals (see later).

Figure 4 illustrates pronounced sexual dimorphism in weight from the beginning of measurements for individuals with unrestricted feeding regimens. It was not possible to determine whether the weight differences by sex were present at birth due to the aforementioned considerations. Considering the final weights recorded at week 92 from Litters II and III combined, the average weight (mean ± SD) was 1 091.0 ± 148.09 g for males (n = 5) and 444.2 ± 59.33 g for females (n = 7) (Student's t-test, $P < 0.0001$).

The Gompertz model parameterization for body weight, based on the averaged weights of males and females from Litters II and III, is presented in **Table** 2. **Figure** 5 illustrates the weight growth of male (n = 5) and female (n = 7) *L. crassicaudata* over 80 weeks, alongside the growth curve fitted to the Gompertz model. The curves, adjusted for the average weights of individuals from Litters II and III, follow a characteristic sigmoidal pattern with a steep initial slope, leading to a subtle inflection point.

The biological interpretation of the Gompertz model concerning the body weight variable is presented in **Table** 3. For *L. crassicaudata*, the parameter A, representing adult body weight, is 2.23 times higher in males than in females. The parameter k_G, which describes the maturation index or specific growth rate, shows similar values for both sexes. The inflection point, T_i, occurs at 24.3 weeks of age for males and 16.8 weeks for females. Parameterization on the Y-axis produced body weight values at the inflection point of 356.3 g for males and 159.6 g for females at the corresponding ages.

The averages of females and males from Litters II + III versus those from Litter I, which experienced partial food deprivation during weeks 47 and 57, are shown in **Figure** 6.

During the ten weeks of food restriction, males lost 170 g of body weight (26% of their body weight), and females lost 75 g (24% of their body weight).

The CG results for the studied animals are presented in **Table** 4. The CG index for males subjected to food restriction was 67%, while females showed a value of 111%, considering their minimum body weight during the restriction period and comparing it with their final weight at week 80. It was observed that males subjected to food restriction achieved partial weight compensation by week 80, whereas females exhibited overcompensation.

DISCUSSION

Young marsupials first appeared in the pouch between 13 and 15 days post-mating, indicating a gestation period of similar duration. This finding is consistent with previous descriptions for *Didelphis virginiana* (McCrady Jr. 1938; Reynolds 1952). This knowledge is crucial to understanding the reproductive cycle of *Lutreolina* since gestation time is a determining factor in planning conservation and management programs for the species. In addition, it allows us to better evaluate the health and well-being conditions of females during this vital period for the survival of their offspring.

The Gompertz curve is characterized by its sigmoidal shape and flexibility, which stem from its inflection point. This model became a preferred regression approach for analyzing growth patterns in various organisms, including mammals and marsupials. Zullinger et al. (1984) examined the growth rates of 331 mammalian species by fitting the Gompertz growth model to published growth curves. Subsequently, Lee & Cockburn (1985) and Cockburn & Johnson (1988) conducted more focused analyses on a range of marsupial species, demonstrating that marsupial growth curves generally conform well to the Gompertz model. In our study, the Gompertz

Table 2

Estimates of the three parameters (mean ± S. D.) of the Gompertz model for the growth of male (n = 5) and female (n = 7) specimens of *Lutreolina crassicaudata.*

	Male	**Female**
Equation	$W_{(t)} = A \cdot e^{(-e^{(-k_G \cdot (t-T_i))})}$	
Number of points	80	80
Parameter A	968.8 ± 22.21	433.8 ± 3.95
k_G parameter	0.05 ± 0.0034	0.06 ± 0.0025
T_i parameter	24.22 ± 0.764	16.82 ± 0.450
Determination coefficient (R^2)	95.28 (P < 0.0001)	98.15 (P < 0.0001)
Interactions	9	4

Table 3

Biological assessment of the parameters of the Gompertz model for body weight in males and females of *Lutreolina crassicaudata.*

	Male	**Female**
Asymptote: $W_{(t)}$ = A (adult weight)	968.8 g	433.8 g
Age turning point: T_i	24.3 weeks	16.8 weeks
Weight at inflection point: $W_{(t)}$ = A/exp	356.3 g	159.6 g

Table 4

Final weight values and compensatory index after 80 weeks in litters of *Lutreolina crassicaudata* with (Litter I) and without (Litter II+III) ten weeks of food restriction.

	Litter I		**Litter II + III**	
Sex	**Male**	**Female**	**Male**	**Female**
N	4	3	5	7
Food restriction (wk)	10	10	–	–
Weight at the beginning of food restriction (week 47) (g)	660.0 ± 21.21	310.0 ± 21.79	–	–
Final weight restricted growth (week 57) (g)	490.0 ± 10.80	235.0 ± 13.23	–	–
Final weight (week 80) (g)	820.0 ± 32.91	495.0 ± 5.00	1.065.4 ± 42.13	432.9 ± 64.42
Compensatory index (%)	67.35	110.63	–	–

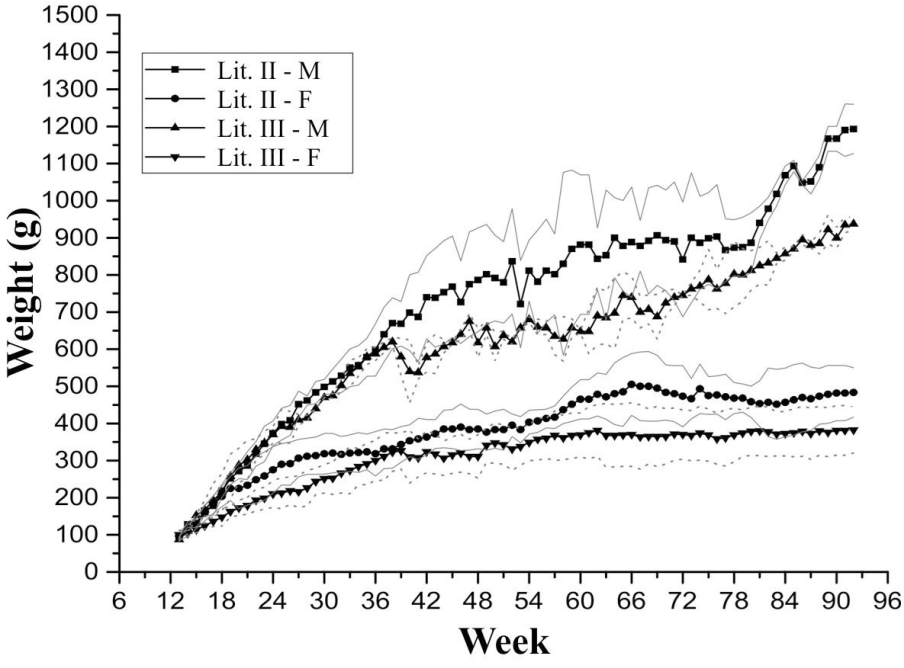

Fig. 4. Weight growth (mean ± S.D.) of males and females of *Lutreolina crassicaudata* from litters II (males, n = 3 and females, n = 3) and III (males, n = 2 and females, n = 4) born in the facility, through 80 weeks from artificial weaning (wk 0 = birth, wk 12 = weaning). Lit. II: litter II; Lit. III: litter III; M: males; F: females.

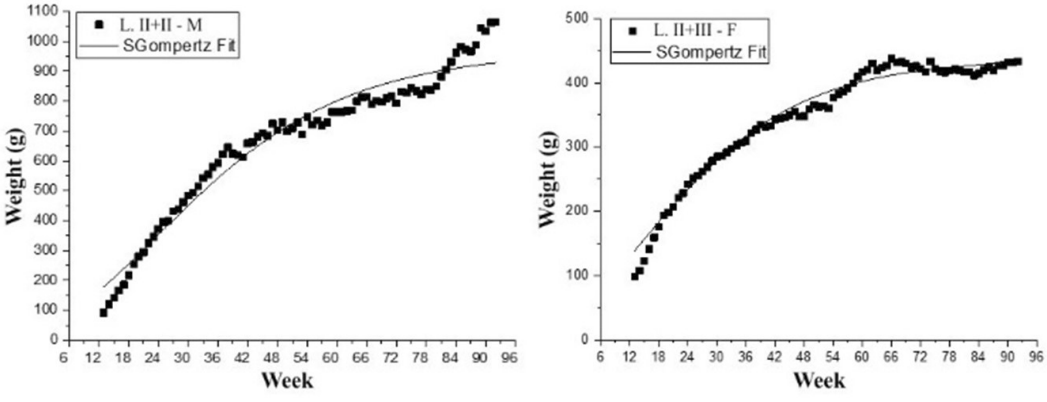

Fig. 5. Average weight growth of male (M, n=5) (left) and female (F, n = 7) (right) *Lutreolina crassicaudata* from Litters II and III (L. II+III), born in the facility, were tracked over 80 weeks from artificial weaning (wk 0 = birth, wk 12 = weaning). A growth curve was fitted using the Gompertz model, with its parameterization detailed in **Table** 2.

model provided a good fit for the growth data of *L. crassicaudata*. However, since weights were not recorded during the pouch stage or the free lactation period, the initial slope of the sigmoidal curve lacks the characteristic gradual increase observed in species where birth weights are available.

In *L. crassicaudata*, the Gompertz model parameter A, representing adult body weight (asymptote: $W_{(t)}$ = A), was higher in males than in females, with estimated values of 968.8 g for males and 433.8 g for females. These values recorded in our captive study are consistent with previous findings reported

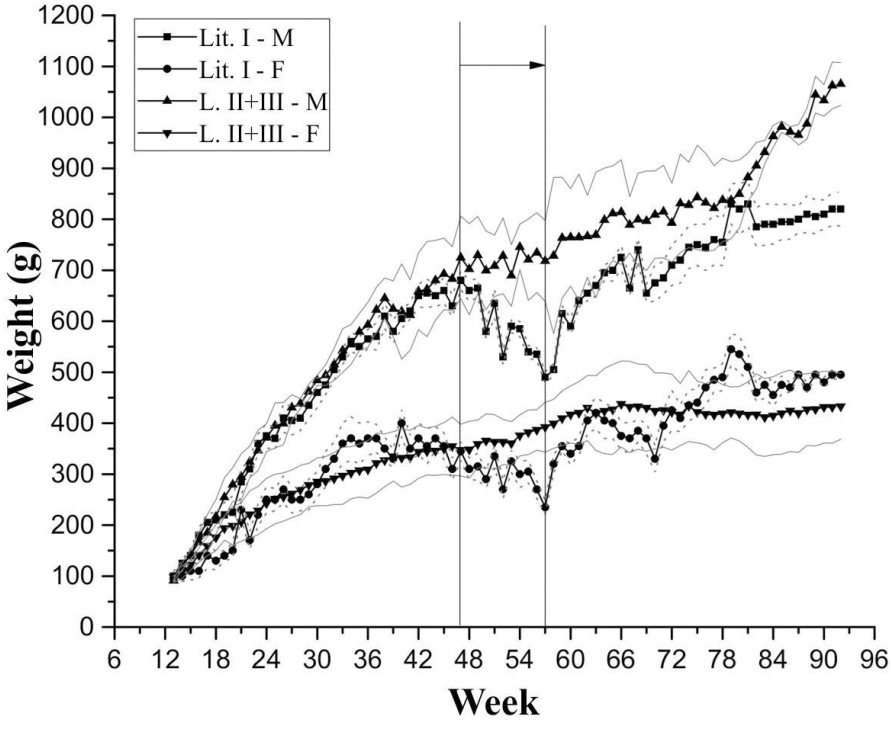

Fig. 6. Weight growth (mean ± S. D.) of males and females of *Lutreolina crassicaudata* born in the facility, comparing the sum of litters II and III (males n = 5; females n = 7) against litter I (males n = 4; females n = 3), through 80 weeks from artificial weaning (wk 0 = birth, wk 12 = weaning). Litter I was exposed to partial food deprivation between 47 and 57 weeks from birth (vertical lines). Lit. I: litter I; L. II+III: litters II + III; M: males; F: females.

by Wilson & Reeder (2005) and Muschetto et al. (2011) under natural habitat conditions. Wilson & Reeder (2005) documented adult specimens weighing between 600 and 1.500 g, though without specifying sex, season, climate, or food availability. Similarly, Muschetto et al. (2011) found mean adult weights of 737.2 ± 339.7 g for males (n = 13) and 490.4 ± 127.1 g for females (n = 12) in a field study conducted in the Autonomous City of Buenos Aires, Argentina, based on multiple captures throughout the year. Despite these similarities, the results of our study differ slightly, likely due to the controlled environmental conditions in our colony, where animals received consistent and homogeneous feeding year-round, mitigating seasonal variations.

The point at which growth acceleration transitions to deceleration marks the inflection point of the growth curve (**Fig**. 1), which often coincides with puberty in many species (Brody 1945; Fowler 1968). In our study, the age and body weight values at the inflection point were higher for males than females. Considering the hypothesis that the inflection point represents puberty, future studies could compare weight gain trajectories and temporal changes in serum sex hormone concentrations (Pittroff et al. 2008).

The inflection point, where $W_{(t)}$ = A/exp at time T_i, reflects the transition in growth rates (Fowler 1968). Our study reveals that the asymmetry of the Gompertz model around the inflection point shows rapid early growth, with females reaching this phase earlier than males. From the model parameters and growth curves, rapid growth phases extended to approximately week 24 for males and week 17 for females, after which the slope of weight gain decreased until about week 80. This marked a stabilization period lasting until approximately week 90 and beyond, with males showing slightly more variability.

This variability might reflect intrinsic factors, including genetics and sex. However, we must also consider the developmental periods described in

the Introduction, which could manifest during this stage. Additionally, the tail of some marsupial species serves as a nutritional reserve, the thickness of which varies depending on the nutritional status of the animal (Ng et al. 1999). Although no significant variations in tail thickness were observed in *L. crassicaudata* hatchlings, future growth studies should include measurements of tail thickness at its base along with body weight and analyze possible correlations.

Adopting this hypothesis of coincidence between the inflection point and puberty —an epoch characterized by profound hormonal changes and well-defined physiological transformations— the data obtained would be crucial for establishing age equivalency between species and among breeds of the same species with different growth rates. This would facilitate growth comparisons across them.

For a given weight, marsupials exhibit a lower k_G value than other mammals (Cockburn & Johnson 1988). The parameter k_G represents the maturation rate of the animals (Nobre et al. 1987), reflecting the speed at which it approaches its asymptotic weight from its initial weight. As the relative growth rate, k_G influences the slope of the growth curve and serves as an indicator of maturity precocity (Nobre et al. 1987); a higher k_G value corresponds to earlier maturation, whereas a lower value indicates delayed maturity (Brown et al. 1976). Consequently, animals with higher k_G values attain their adult weight more quickly than those with comparable initial weights but lower k_G values. In our study, the k_G value for *L. crassicaudata* falls within the expected range for marsupials (Lee & Cockburn 1985; Cockburn & Johnson 1988). Additionally, growth rates estimated through the model are comparable between males and females in this species, suggesting that both sexes exhibit similar maturity precocity.

Although the curves generated from the Gompertz model exhibit a well-fitted sigmoid shape, **Figure** 4 reveals relative variability. This variability is evident from the standard deviations among organisms of the same sex and litter, kept under identical environmental conditions. This phenomenon suggests variability of genetic origin (Bruijning et al. 2020; Ferchichi et al. 2022). This hypothesis must be corroborated through other techniques (such as isoenzymes) to better determine the type and magnitude of potential polymorphism. Such characteristics, along with their influence on plasticity under selective pressures, indicate that *L. crassicaudata* would respond significantly to selective breeding pressures aimed at developing purebred lines (inbred or outbred).

Figure 6 illustrates a comparison of average weight growth between females and males from Litters II and III relative to those in Litter I. The latter underwent a 20% reduction in their habitual ration for ten weeks, between weeks 47 and 57 of life. In the early weeks, weight gain was similar across groups and litters. However, this congruence was disrupted with dietary variation. The weight curve for females and males in Litter I shows a decline with fluctuations during the food restriction period. Upon resuming their regular diet at 57 weeks, a compensatory phase was observed, rapidly elevating the weights of the study animals to levels comparable to or even exceeding those of Litters II and III. This phenomenon aligns perfectly with the concept of "catch-up growth" (Finkielstain et al. 2013).

Data from **Table** 4 and **Figure** 6 reveal that the CG behavior of the studied animals aligns with results obtained for other mammalian species (Drouillard et al. 1991a; Owens et al. 1993; Hornick et al. 2000), albeit with some peculiarities.

After nutritional restriction and subsequent refeeding, animals exhibit varying CG responses (Morgan 1972; Tudor & O'Rourke 1980; Hornick et al. 2000). Compensation can be complete or partial. In the former, animals achieve the same weight for age as those not subjected to restriction. In the latter, animals increase weight gain during refeeding but fail to reach the same values as unrestricted animals within the same timeframe. These two responses are most commonly observed. Another less frequent response is non-compensation, typically occurring when nutrient restriction happens at an early age.

In the studied marsupials, the compensatory index for males and females subjected to food restriction was 67% (undercompensation) and 110% (overcompensation), respectively, based on minimum weight during the restriction period compared to weight at 80 weeks. This highlights a difference between sexes in weight loss-recovery dynamics, possibly linked to hormonal factors and body nutrient storage, particularly in the tail of females. During CG, undercompensation is more common than overcompensation.

The magnitude of CG depends on the growth phase or age at which undernutrition occurs, with early-stage restrictions being more detrimental than those in later stages (Wilson & Osbourne 1960), potentially precluding compensation. Numerous studies reveal a total or poor CG when animals experience early-life restrictions (Morgan 1972; Tudor

& O'Rourke 1980; Hornick et al. 2000). At an early age, undernutrition can irreversibly affect normal growth. Similarly, severe maternal undernutrition during gestation can permanently reduce fetal size.

In more advanced growth stages, an inverse relationship has been found between the growth rate during rehabilitation and the rate of gain during undernutrition. Naturally, greater CG occurs with higher nutritional levels during rehabilitation (Álvarez-Zapata & Benezra 2004).

In *L. crassicaudata*, despite the animals being relatively young (one year old), females subjected to ten weeks of dietary restriction achieved complete compensation, reaching a final weight 14.4% higher than females from unrestricted litters and a compensatory index of 111%. Conversely, although males showed a recovery trend (compensatory index = 67%), compensation was partial, with their final weight remaining 23% below that of unrestricted animals.

The response to refeeding is influenced by the severity and duration of dietary restriction, with more severe restrictions resulting in lower initial weight during the compensatory phase and greater relative weight gain during restitution (Wilson & Osbourne 1960). The forms of restriction are categorized as: a) severe, resulting in live weight loss; b) maintenance, keeping live weight constant; and c) moderate, producing subnormal live weight gain (Wilson & Osbourne 1960). A shorter and less severe dietary restriction yields better CG.

Not only does restriction severity matter, but also the poor quality of the diet during compensation can also hinder CG (Ryan et al. 1993).

The extent and severity of dietary restriction can result in a lack of compensation or variable responses in CG. Many studies have demonstrated that full CG is possible if the restriction is not too severe (Doyle & Leeson 2003); in alpacas, full CG was achieved with moderate restriction (Olazábal et al. 2009). In our study, dietary restriction was severe (20% less than the usual amount of food for ten weeks), leading to an average weight loss (compared to the other two groups) of 25% across both sexes. Subsequently, weight was fully recovered over the next 20 weeks without complications. One of the main issues preventing firm conclusions about these two factors individually is the inability to separate the concomitant effects of the severity and duration of dietary restriction from restricted growth itself (Lawrence & Fowler 2002).

CG can exhibit variability in observed responses within and between species, suggesting a close interplay among nutritional, physiological, and genetic factors (Hornick et al. 2000; Álvarez-Zapata & Benezra 2004; Finkielstain et al. 2013; Jones & German 2013; Griffin 2015; Deng et al. 2024). This response is associated with (a) the transformation and utilization of food during the compensatory phase; (b) reduced maintenance requirements; (c) increased food intake; (d) high efficiency in food utilization; (e) changes in the composition of weight gain; and (f) alterations in endocrine status.

The relevance of our findings extends beyond the scope of laboratory animals and can be linked to the rehabilitation and refeeding of recovering wildlife. In this regard, Tardieu et al. (2020) analyzed the maintenance and reproduction of *D. marsupialis insularis* under rehabilitation conditions, highlighting the importance of nutrition for offspring viability. In their study, the death of the only neonate that managed to reach the maternal pouch was attributed to starvation, underscoring the necessity of ensuring adequate feeding for recovering individuals. In relation to our study, the CG observed in *L. crassicaudata* suggests that proper refeeding could enhance the survival and development of wildlife offspring that have experienced periods of nutritional restriction, such as those separated from their mothers during rehabilitation.

On the other hand, Lunney et al. (2004) evaluated the rehabilitation and reintegration of koalas affected by wildfires, finding that rehabilitated individuals exhibited survival rates similar to those of unaffected koalas. This suggests that, as in our study with *L. crassicaudata*, physiological recovery capacity is a key factor in wildlife rehabilitation. CG in marsupials could play a crucial role in the restoration of populations affected by adverse events, allowing for the recovery of physical condition following periods of starvation or nutritional stress.

Taken together, our findings on CG in *L. crassicaudata* provide valuable insights for wildlife rehabilitation. Future studies could assess whether this physiological response is similarly expressed in other marsupials and how environmental conditions influence its manifestation. Additionally, understanding the mechanisms regulating CG could be useful for optimizing rehabilitation strategies in threatened species and improving the effectiveness of conservation programs based on refeeding and reintegration of individuals into their natural habitats.

Additionally, CG holds significant practical importance and interest in production animals (Drouillard et al. 1991a; Mitchell 2007). This process occurs when animals subjected to periods of undernutri-

tion demonstrate the ability to regain their normal growth trajectory once provided with adequate food in both quantity and quality. Several explanations for CG have been proposed (Hornick et al. 2000; Deng et al. 2024), though the underlying mechanisms remain poorly understood, and the biochemical and physiological processes driving these accelerated growth rates are only partially elucidated. Álvarez-Zapata & Benezra (2004) proposed that CG in production animals could be explained by several factors: (a) an increased feed intake among rehabilitating animals compared to those with normal growth of similar weight, (b) higher feed conversion efficiency, and (c) lower maintenance requirements.

CONCLUSIONS

The growth of *L. crassicaudata* observed in this study exhibited a clear sexual dimorphism, with greater growth in males compared to females, and demonstrated a strong fit to the Gompertz growth model.

When analyzing the values presented in this work, it is important to note that they were obtained under strict captivity and laboratory conditions, with specialized maintenance and feeding facilities. These findings should be compared with similar studies conducted in field conditions or under confinement for animal production to determine whether differences exist between these scenarios.

Further research would be desirable to confirm these growth data for other species related to *L. crassicaudata* and to determine whether CG is a generalized physiological response among eutherians and metatherians, rather than being limited to species associated with animal production or human children. Additionally, it would be valuable to explore whether this physiological phenomenon represents a natural response to environmental nutritional changes (due to natural disasters, droughts, etc.) in mammals.

Finally, it can be inferred that this original study will not only be of interest to the field of non-traditional laboratory animals (NTLAs). Besides contributing to the knowledge of the biology and husbandry of *L. crassicaudata* in laboratory settings, our findings may provide new insights into CG, relevant both for production animals and for understanding catch-up growth in children.

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ONLINE SUPPLEMENTARY MATERIAL

Table S1
Table S2
Table S3
Table S4